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Optimal foraging on perilous prey: risk of bill damage reduces optimal prey size in oystercatchers

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Intake rate maximization alone is not always sufficient in explaining prey size selection in predators. For example, bivalve-feeding oystercatchers regularly select smaller prey than expected if they aimed to maximize their intake rate. It has been proposed that to these birds large prey are "risky," in the sense that birds may damage their bills when feeding on large bivalves. Large bivalves yield more energy, but according to this hypothesis this is achieved at the expense of energy yield in the long term when (1) the risk of bill damage increases with prey size and (2) foraging with a damaged bill is less effective. In accordance with this hypothesis, we show that captive oystercatchers feeding on large cockles experienced a high probability of bill tip damage, while bill damage was absent when cockles were small. Moreover, among free-living oystercatchers the prevalence of bill damage was correlated with mean cockle size near the capture site, and the data on captive birds fit in this pattern. Food intake of captive oystercatchers feeding exclusively on cockles was reduced by 23% after bill damage, and free-living birds with damaged bills had 14 g lower mass. Because lower body mass was associated with higher mortality probability, these results indicate long-term costs associated with feeding on large cockles. We conclude that the risk of bill damage can potentially explain why oystercatchers avoid large bivalves and that oystercatchers may maximize long-term intake rate by selecting prey sizes that are "suboptimal" from a short-term rate-maximizing point of view. *Key words:* prey choice, prey profitability, prey size selection, risky prey. *[Behav Ecol 17:297–302 (2006)]*

Prey choice has large consequences for both prey and predator populations, and the mechanisms underlying prey selection may be important to understand the behavior (e.g., predator distribution pattern, prey growth strategy) and population dynamics of predators and their prey (Paine, 1966). Most prey-selection studies have adopted an optimality approach to understand prey choice, initiated by the work of, among others, Emlen (1966), MacArthur and Pianka (1966), and Pulliam (1974); see Stephens and Krebs (1986) for an overview. It has been predicted that foraging predators that aim to maximize their long-term average energy intake should always accept prey items into their diet with a profitability (defined as yield divided by handling time) higher than their long-term average intake rate (Charnov, 1976; Pulliam, 1974). However, in a host of systems, predators typically select smaller prey than expected from prey profitability, for example, in arthropods feeding on caterpillars (e.g., Cogni et al., 2002), crabs and whelks feeding on bivalves (Dietl, 2003; Juanes, 1992), cannibalistic salamander larvae feeding on their conspecifics (Elgar and Crespi, 1992), and sexually cannibalistic arachnids selecting mates (e.g., Johnson, 2005). One hypothesis proposed to explain why larger prey items (or, in the case of the arachnids, mates) are rejected as prey despite the fact that alternative preys have lower profitability is that predators are constrained by the higher risks associated with larger prey. According to this "risky prey hypothesis," the risk of, for instance, damage to the feeding apparatus increases with prey size, and damage to the feeding apparatus reduces intake rate, and these processes combined result in a trade-off between long-term and short-term intake rates.

Although the risky prey hypothesis has been proposed to explain apparent discrepancies between prey profitability and prey size selection for several systems, for example, molluscivorous crabs (Smallegange and van der Meer, 2003) and caterpillar-feeding arthropods (Cogni et al., 2002), evidence for this hypothesis is often incomplete and/or circumstantial. For instance, Dietl (2003) showed that the risk of shell damage to the busyconine whelk *Sinistrofulgur sinistrum* preying on the bivalve *Mercenaria mercenaria* increased with increasing prey size but did not report whether this reduced intake rate. We are not aware of a study that tested both components of the risky prey hypothesis.

In molluscivorous oystercatchers *Haematopus ostralegus* L. prey profitability generally increases with prey size (Zwarts et al., 1996b), but birds often reject the largest size classes, despite their high profitability. For instance, oystercatchers switch to feed on small mussels *Mytilus edulis* L. and cockles *Cerastoderma edule* L. in spring, even when more profitable larger prey are available (Cayford and Goss-Custard, 1990; Ens et al., 1996). Cockle-feeding oystercatchers accepted the large-size classes only in late winter, when energy demands were high (Norris and Johnstone, 1998). Sutherland (1982) and Norris (1999) both found that oystercatchers preferred smaller cockles than expected on the basis of their profitability and abundance (Figure 1). If the risk of bill damage increases with increasing prey size and if foraging is less effective with a damaged bill, then this would reduce optimal prey size below the value expected on the basis of short-term rate maximization alone (Hulscher, 1996; Johnstone and Norris, 2000; Zwarts et al., 1996a,b). Although the risky prey hypothesis is plausible, there is to our knowledge no direct evidence for effects of bivalve shell size on bill tip damage or effects of bill

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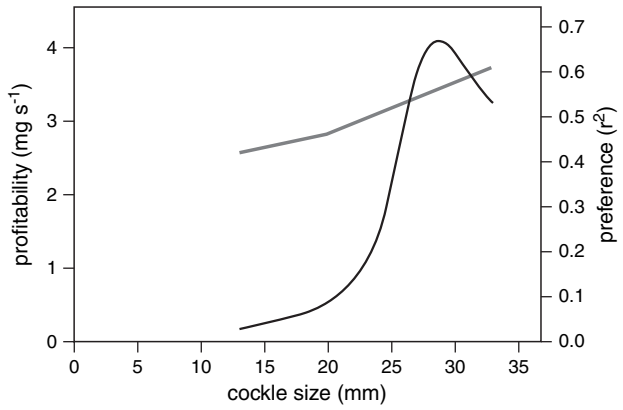

Figure 1
The profitability (yield in mg AFDM per second handling) of cockles (gray line) and the preference of oystercatchers (black line) as a function of cockle size (from Sutherland, 1982). Preference is expressed as the correlation coefficient between the rate at which cockles of a certain size are taken and their density in the substrate. Thus, higher correlations indicate stronger preference.

tip damage on subsequent intake. Indirect evidence for the bill damage hypothesis was found by Sutherland (1982), who showed that oystercatchers rejected cockles that they had to dislodge from their bills and that this proportion increased with shell size. In this paper, we test both components of the risky prey hypothesis for cockle-feeding oystercatchers; that is, whether the incidence of bill tip damage is related to prey size and whether bill tip damage affects intake rate and condition. Firstly, using captive oystercatchers foraging on two different cockle size classes, we tested the effect of prey size on bill damage incidence and the effect of bill damage on total food intake. Secondly, using captures of free-living oystercatchers at multiple sites, we tested the effect of cockle size on the prevalence of bill tip damage and whether there was a mass difference between birds with damaged and undamaged bills.

METHODS

Captive birds

In 1996 and 2000, we conducted experiments with cockle-feeding, captive oystercatchers. Single birds foraged on live cockles in a 50 m^2 tidal cage (Swennen et al., 1989) for periods of up to 3 weeks. The tidal regime was set to two 5-h feeding periods per 24 h. Total intake per 24-h period was derived from empty-shell counts, and eaten cockles were replaced daily by fresh cockles from a stock of live cockles kept in a gully. In 1996, the average length of cockles offered in the tidal cage was 23.9 mm (close to mean cockle size in the field, see below), with an average energy content of 147 mg ash-free dry mass (AFDM) per cockle. Handling time for these cockles was on average 77.6 s, resulting in a profitability of 1.90 mg AFDM/s on average. Cockles offered in 2000 were on average 36.9 mm—54% longer than in 1996 and at the upper tail of the size distribution of cockles in the field—and contained 684 mg AFDM per cockle. With an average handling time of 245.4 s, this made the profitability of these cockles 47% higher at 2.79 mg AFDM/s. Our captive oystercatchers all used the stabbing technique to open prey, where they stab their bill between both valves of the prey and cut the adductor muscle.

Birds were weighed and the state of their bills was examined almost daily. Birds were removed from the experiment when their weight dropped below 400 g and given opportunity to recover by feeding on freshly thawed dead cockles. The bill was considered damaged if upper and lower bill were not of the same length at the bill tip. In most cases of bill damage, the length difference between both mandibles was 1–2 mm. All but four birds were removed from the cage when bill tip damage occurred. These four birds were in very good condition when damage occurred. We used these four birds to examine the effect of bill damage on foraging success of birds in good condition. Bill tip damage risk was calculated using Kaplan-Meier survival analysis, treating the occurrence of bill tip damage as "death."

Free-living birds

Data on free-living birds were collected at different sites around the Dutch Wadden Sea in February 2001 and in the period between November 2002 and March 2003. See Verhulst et al. (2004) for methods. In brief, birds were captured using cannon nets and immediately ringed, measured, and subsequently released. Biometric parameters were measured following standard techniques. Following Hulscher (1985), we classified bill tip shape using the following categories: sharp, intermediate, and blunt. Among blunt-billed birds, we discriminated chiselers and hammerers on the basis of the bill tip width. Sharp and intermediate bill tips are associated with diets of soft-bodied and/or thin-shelled prey, while blunt bills are found on birds feeding predominantly on thick-shelled bivalves like cockles and mussels. The widest bills in this group belong to hammerers, which break into bivalves by hammering a hole in the shell. Chiselers mainly use the stabbing technique, where the bill is stabbed into a slightly gaping shell after which the shell is prised open (Hulscher, 1996; Norton-Griffiths, 1967).

Bill damage was scored as the asymmetry (in mm) between the upper and lower mandible. Only birds with a chisel-shaped bill were included in the analyses in this paper because these birds predominantly use the stabbing technique. Furthermore, all captive oystercatchers were stabbers, and we wanted to compare the field results with the laboratory results. Moreover, birds using the hammering technique were relatively scarce in our study area (8% and 5% in both study years, respectively), and in the first year none of these had an asymmetric bill tip. Birds were sexed on the basis of bill morphology which yields the correct sex in 87% of the cases (Zwarts et al., 1996d).

The relation between prey size and the prevalence of bill tip damage was analyzed using logistic regression. As estimate of cockle size, we used the mean cockle size in a circle with a radius of 5 km centered on the capture site. These data were collected by the Netherlands Institute for Fisheries Research (RIVO), see Bult et al. (2004) for methods. We used data from the annual survey conducted in May, a few months after we captured the oystercatchers, because this is the best estimate available. The previous year's cockle spat was excluded from the calculation of mean cockle size because cockle spat is generally too small to be eaten by oystercatchers. The RIVO survey yields data on fresh mass of cockles, while in most other studies and our experiments with captive oystercatchers maximum shell length was used. For comparability we therefore converted the fresh mass data to cockle size using the equation reported by Bult et al. (2004), where prey length $= 2.67 + 0.308 \times \ln(\text{freshweight in g})$.

The association between mass and bill tip damage was analyzed using multiple regression, controlling for the following variables to increase the power of the analysis: capture occasion (fixed factor), time elapsed between capture and weighing (expressed as proportion of 24 h), and body size. To simplify the model, we combined biometric variables using principal component analysis to obtain one estimate of body size. We used the first principal component, which was approximately equally loaded with wing length, "tato" (total

length of tarsus plus the middle toe), and two bill measurements (bill length and height). We further included minimum age (range of 2–5 "calendar" years), estimated on the basis of plumage, bill, eye, and leg characteristics. However, more detailed analysis revealed that with respect to age there was only a difference between yearlings and older birds, and no further age effect was detectable among birds older than 1 year. We therefore replaced age with yearling as a dummy variable in the model.

RESULTS

Captive birds

In 1996, when cockles were small, no bill tip damage was noted at all, so the risk of bill tip damage was approximately zero. In 2000, when cockles were large, Kaplan-Meier analysis showed that the mean survival "time" (i.e., the number of cockles a bird could open before it damaged its bill) was 74.4 ± 9.6 cockle (Figure 2). This indicates very low bill "survival," given that a captive oystercatcher would need approximately 48 cockles of this size to meet its daily energy requirement (Zwarts et al., 1996c). The risk of damaging the bill tip was 0.01 per cockle eaten.

Most birds were removed from the experimental cage when bill tip damage occurred, but we have data on four birds feeding with an intact as well as with a damaged bill. Total intake was quantified as the number of cockles eaten during one low-water period. The data were skewed toward low values (including a few cases where total intake was zero), and therefore we ln(total intake + 1)–transformed the data prior to analysis. Birds consumed fewer cockles per low-water period when feeding with a damaged bill than when their bills were undamaged (Figure 3, general linear model with individual as factor, $F_{1,63} = 5.67$, $p = .02$). Although cases in which birds foraging with a damaged bill always followed those foraging with an intact bill, it is unlikely that the decreased intake for birds with damaged bills was a time effect as there was no decrease in total intake with time spent in cage for birds with intact bills ($F_{1,59} = 0.21$, $p = .6$). On average, the total intake of a bird feeding with a damaged bill was 77% of its total intake with an intact bill.

Free-living birds

Oystercatchers were captured in two winters, and the proportion of birds with a chisel bill tip—associated with using the stabbing technique to open bivalves—was lower in the second winter (29.5% [$n = 515$] versus 15.7% [$n = 532$]; $\chi^2 = 28.2$, df = 1, $p < .001$). The prevalence of damaged bills was higher in the second winter (for chisel-tipped birds: 15.8% versus 33.3%; $\chi^2 = 9.7$, df = 1, $p < .002$). Birds with a "hammer bill tip"—associated with using the hammering technique to open bivalves—were comparatively rare in both winters (8.0% and 4.7%, respectively). Of all birds with a hammer bill tip ($n = 61$), there were eight birds in which the bill tip was damaged, all in the second winter. This number is insufficient to allow statistical analyses of this group, which is another reason (next to the comparability with the captive birds which all had chisel bill tips) why further analysis was restricted to birds with chisel bill tips. Among all birds with damaged bill tips, the (absolute) difference in length between upper and lower mandible was 2.26 mm (SE = 0.14, $n = 41$) in the first winter and 1.27 mm (SE = 0.03, $n = 202$) in the second winter.

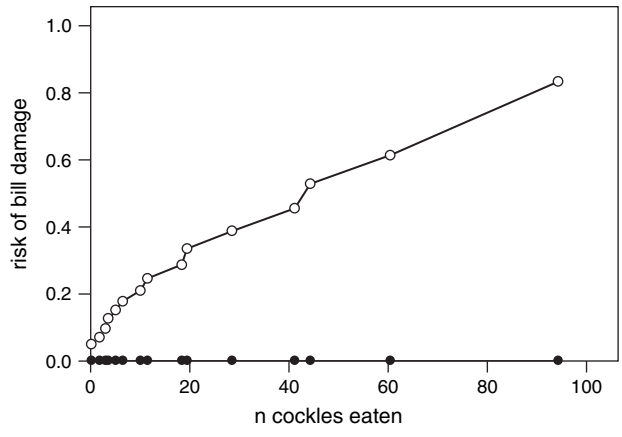

Figure 2
Hazard function for birds feeding on small (black markers) or large (white markers) cockles.

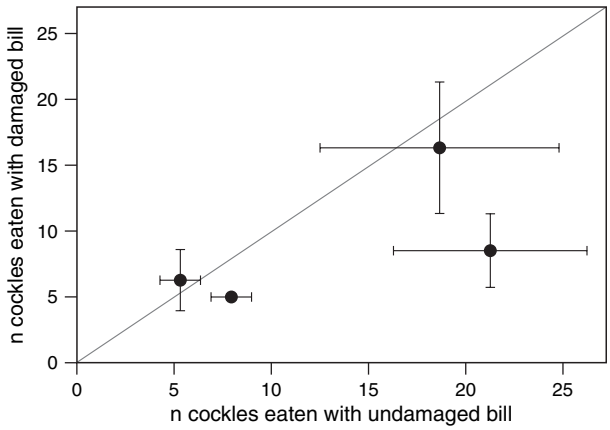

Figure 3
The difference in the number of cockles eaten during one low-water period for four birds foraging repeatedly with an intact bill versus the intake for these same birds when foraging with a damaged bill tip ± SE. Line: y = x.

The relationship between mean cockle size and the proportion of birds with a damaged bill tip was analyzed using logistic regression using each capture as a unit in the analysis. One site (Vlieland, 2003) was omitted, because cockles were fished near the capture site around the time of the capture, prior to the cockle survey in May after the capture. Consequently, we have no relevant estimate of the size of the available cockles. The proportion of birds with a damaged bill tip increased with cockle length (Figure 4; $F_{1,7} = 54.8$, $p < .001$, proportion damaged = $e^a/(1 + e^a)$, where $a = -13.3$ [3.31] + 0.44 [0.12] × length in mm [SE]). Year of capture, total cockle biomass available, and the interaction between cockle size and cockle mass available did not significantly decrease the deviance (all $p > .5$) when added to a model containing cockle length. We used cockles measured within a 5-km radius around the capture site for this analysis, but using cockles measured in a 2-km radius yielded the same results.

To investigate whether birds with a damaged bill tip had lower mass, we selected all captures that included birds with bill tip damage ($n = 8$ captures, 197 chisel-tipped birds of which 52 had a damaged bill tip). The multiple regression analysis (Table 1) revealed that birds with damaged bill tips had 14 g lower mass when compared with birds with undamaged bill tips (Figure 5). Sex was not significant when added to this model and therefore not included. On inspection of Figure 5, it appears that the effect was much stronger in the first season (winter 2000–2001) than in the second season

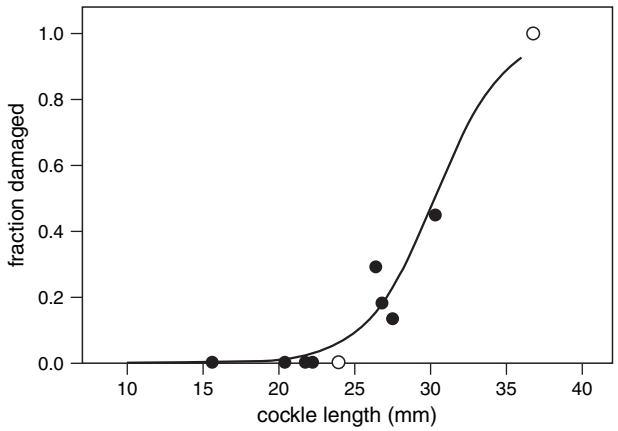

Figure 4
Bill tip damage prevalence increased with cockle length at the capture site. Closed circles, field data; open circles, cage data. Note that only the field data were used in the calculation of the regression line and statistical test. Given the high probability of bill tip damage when captive oystercatchers were feeding on large cockles (0.01 per cockle) and the recovery time of a damaged bill tip, we inferred that in a population feeding on cockles of 37 mm all birds would permanently have bill tip damage.

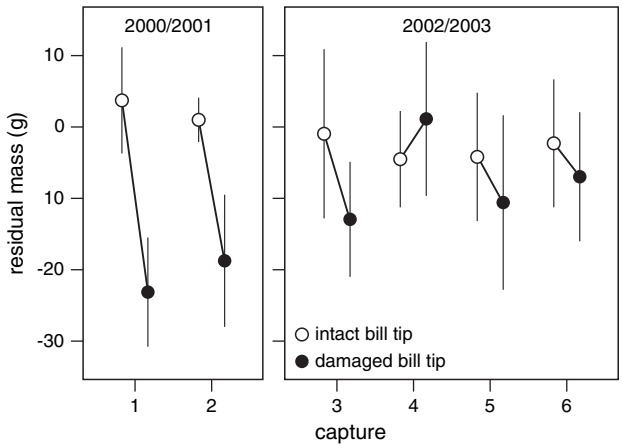

Figure 5
Bill tip damage and body mass in different captures. Body mass (+SE) shown is the residual calculated using all parameters in Table 1 except bill tip damage. Numbers on the abscissa indicate chronological order of capture, with the exception of capture 6 which comprises data from three different captures, each with low sample size (these captures were not pooled in the analysis). Sample sizes (intact/damaged) are 26/10, 64/14, 11/9, 21/6, 8/9, and 15/4 for captures 1–6, respectively.

(winter 2002–2003). We tested this by adding the interaction between year and bill tip damage to the model in Table 1. This interaction term approached significance ($F_{1,183} = 3.3$, $p = .07$), and the estimated effects of bill tip damage on mass were −22.6 and −4.2 g in the first and second seasons, respectively.

DISCUSSION

Foraging oystercatchers and other animals regularly select prey that are smaller than the size with which they would maximize their short-term intake rate (e.g., Figure 1). It has repeatedly been hypothesized that this is due to an effect of prey size on the risk of damage to the feeding apparatus (e.g., claws in crabs [Juanes and Hartwick, 1990], bill tip damage in oystercatchers [Hulscher, 1996]), assuming that such damage reduces foraging success (the risky prey hypothesis). In accordance with this hypothesis, we showed that captive oystercatchers had a much higher risk of damaging their bills when feeding on large (average length 36.9 mm) cockles than oystercatchers feeding on medium-sized (average length 23.9 mm) cockles (Figure 2). This finding was confirmed with data of incidence of bill tip damage in free-living oystercatchers, which was higher when cockles were larger (Figure 4), indicating that the risk of bill tip damage increased with cockle size. It is worth noting that the data on captive birds fit well in the pattern observed among free-living birds (Figure 4), which supports the interpretation that there is a causal relationship between cockle size and prevalence of bill tip damage.

The implicit assumption of the risky prey hypothesis that bill damage reduces foraging success was also supported: the number of cockles consumed per tidal cycle was reduced by 23% following bill damage in captive oystercatchers (Figure 3), and free-living oystercatchers had lower mass when their bill tip was damaged (Figure 5). The mass difference between birds with and without bill tip damage under natural conditions could be caused by an unknown third factor instead of being causally related to the observed damage. For example, some birds could be more proficient foragers, resulting independently in higher mass and less bill tip damage. The data on captive birds are of importance in this context because we observed an effect of bill tip damage on total intake within individual birds (Figure 3), which indicates a direct effect of bill tip damage, rather than an effect of a confounding third factor. Due to the nature of our data on intake rate, it was not possible to determine which components of the foraging cycle were most affected by bill tip damage, leading to the reduction in total intake. It seems plausible that handling time increased because a damaged bill is probably suboptimal for opening cockles, and in particular cutting the adductor muscle may be more difficult with an asymmetric bill tip. It seems likely that in addition oystercatchers feeding with a damaged bill became more selective, to avoid more bill damage, which would increase search time per consumed food item. Further experimentation is required to resolve this issue.

The effect of bill tip damage on nutritional state is likely to depend on the availability of alternative prey of which profitability may be less affected by bill tip damage. For the captive oystercatchers there was no alternative prey, but for the free-living birds we found that the effect of bill tip damage on mass was much stronger in the first season (−22.6 g), as compared with the second season (−4.2 g; although the interaction bordered on significance). This would suggest that oystercatchers

Table 1
Multiple regression analysis of the association between mass (g) and bill tip damage (0 = intact, 1 = damaged)

Variable	Coefficient (SE)	F	p
Constant	607.9		
Capture		4.9	.001
Hold time	−240.7 (60.5)	15.8	.001
Hold time^2	205.0 (77.2)	7.1	.009
Body size	12.7 (1.7)	54.8	.001
Yearling	−32.4 (5.6)	33.4	.001
Bill damage	−13.8 (5.1)	7.4	.007

Yearling = 1 for 1-year-old birds and yearling = 0 for older birds. Hold time is time elapsed between capture and weighing in proportion of 24 h. p values are based on removal of the term from the model containing all accepted terms. $r^2 = .59$, $n = 197$. Coefficient of the constant is the (weighted) mean across capture sites. The df for the F tests are 7,184 for capture and 1,184 for all other tests.

relied to a large extent on cockles in particular during the first season, which is in agreement with the strong effect of cockle fisheries on oystercatcher condition we observed in that year (Verhulst et al. 2004). Moreover, it is known that at least one important alternative prey species (mussel *Mytilus edule*) was more abundant in the second season than in the first season (Ens et al., 2004), and we do not know whether bill tip damage also reduces intake rate when feeding on mussels.

Summarizing, both aspects of the risky prey hypothesis were confirmed by our data. The probability of bill damage increased with cockle size, and bill damage resulted in lower intake rate and lower condition. This indicates that at least part of the suboptimal prey choice can be explained by the risky prey hypothesis, but we acknowledge that other processes may also contribute to the observed preference pattern. For example, larger cockles may be avoided because they have a higher parasite load (Norris, 1999), and rejecting cockles may therefore be a way to avoid getting parasitized.

Optimal prey size

To assess quantitatively to what extent the bill damage hypothesis explains selection of prey that are smaller than expected when net rate is maximized, we will now try to quantify how the effect of bill tip damage risk affects optimal prey size, although we recognize that this exercise remains somewhat speculative.

When calculating prey size that maximized long-term intake rate, we assumed that (1) the relationship between cockle size and profitability as described by Zwarts et al. (1996b) is representative for oystercatchers feeding with an intact bill, (2) that the effect of bill tip damage on intake rate is caused by an increase in handling time only, and (3) that the effect of bill tip damage on profitability is independent of cockle size. If we take into account that the total intake of captive birds foraging on large cockles with damaged bills was 0.77 of their intake with intact bills, we can calculate that prey profitability decreases with 0.77 (prey yield stays the same, but handling time increases by 1/0.77, hence profitability decreases by a factor 0.77; using Holling's disc equation to calculate the change in handling time yields the same value). This calculation yields profitability curves for birds foraging with intact and damaged bill tips (Figure 6), and the realized profitability will lie between these curves, the precise position depending on the frequency of bill tip damage. We know the proportion of birds with a damaged bill as a function of mean cockle size (Figure 4), and this proportion can also be taken to be the proportion of time that the average oystercatcher forages with a damaged bill. This proportion was incorporated in the profitability estimates by calculating the mean profitability for intact and damaged bills, weighted for the time that the bill is damaged. The profitability curve that includes the effect of bill tip damage shows a plateau starting at roughly the same cockle length at which Sutherland (1982) found peak preference (Figure 6). This suggests that the risky prey hypothesis may be quantitatively important enough to explain the rejection of large bivalve prey that would yield a higher profitability than prey that are accepted.

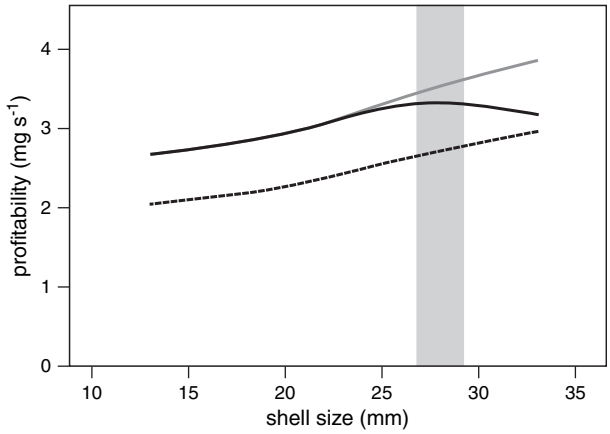

Figure 6
Profitability as a function of cockle size as calculated by Zwarts et al. (1996b) (solid gray line), the minimum profitability if probability of bill tip damage is 1 (dashed line), and the mean profitability when the measured occurrence of bill tip damage is taken into account (solid black line). Gray area indicates preferred size range as observed by Sutherland (1982).

We assumed that the decrease in profitability after bill damage was independent of cockle size, but this assumption has little influence on the shape of this curve before reaching the plateau as the incidence of bill tip damage for birds feeding on cockles of 25 mm and smaller was negligible. However, plateau length is influenced by the exact shape of the relationship between cockle length and the assumed increase in handling time (and decrease in profitability) for birds feeding with damaged bill tips. If the decrease in profitability is larger for larger cockles, the plateau will be longer. Profitability may still increase again with increasing cockle length after the plateau, but because cockles with a length >40 mm are rare (e.g., Ens et al., 1996; Zwarts et al., 1996a,b), this part of the size range has little biological relevance.

Foragers are not only sensitive to the mean profitability but also to the variance (Kacelnik and Bateson, 1996). Over the size range where oystercatchers forage with a damaged bill for part of the time the long-term variability in profitability is higher than when bills are always intact or always damaged. Bill tip damage reduces the maximum attainable intake rate, which is a risk when conditions suddenly become harsh. Consequently, we would expect that oystercatchers prefer the smaller cockles when choosing between sizes that are within the profitability plateau.

An increase in risk to predators with increasing prey size has been hypothesized to affect prey size selection in a wide range of systems (see Introduction). Thus, oystercatchers and other animals face a trade-off between short-term intake rate and long-term intake rate, and the (risky) option only becomes attractive under harsh conditions (e.g., cold weather), when short-term intake is more important than long-term intake. For example, oystercatchers with deformed bills are overrepresented in samples of cold spell victims (Swennen and Duiven, 1983), and under harsh circumstances up to 60% of wild oystercatchers can show small bill deformations (Swennen et al., 1983). These numbers in combination with our findings indicate that the risk of bill damage is likely to be an important consideration in diet selection of cockle-feeding oystercatchers.

The oystercatchers are one of the model species for the development of individual-based population models that are used to predict population dynamics of predators and their prey and habitat distribution (e.g., Stillman et al., 1997, 2002). It seems likely that when such models are applied to cockle-feeding oystercatchers, they would benefit from the incorporation of the trade-off between short and long-term intake rates, in particular when examining effects of harsh circumstances that result in, for example, high energy expenditure (cold weather) or short available foraging time due to, for example, high sea levels because it is under these circumstances that oystercatchers may experience problems meeting their energy demands.

The avoidance of large prey by predators also has consequences for the prey, in particular for species such as bivalves and fish that continue to grow throughout their life, because it puts a premium on reaching a large size early in life. Because there is usually a trade-off between growth and reproduction (Kozlowski, 1996; Stearns, 1992), avoidance of large-size classes by predators will shift optimal age/size to start reproduction to higher values. Such evolutionary responses will in turn impose a selection pressure on predators to be able to cope with larger prey, and as such our findings uncover what is likely to be but one small component of the arms race between predators and their prey.

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